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STAGES IN THE EMBRYONIC DEVELOPMENT OF THE ATLANTIC SALMON *SALMO SALAR L.*

1. CRITERIA FOR DISTINGUISHING THE STAGES OF DEVELOPMENT

by

Yu. N. Gorodilov

The concept of embryonic development stages. The notion of embryonic development stages is still a subject of debate. On the one hand, it is thought that changes in temperature often result in departures from the sequence in which morphological characters normally appear, or, in other words, that heterochronism is a widespread phenomenon (Lyubitskaya, 1934; Hayes et al., 1953; Meshkov, Lebedeva, 1977; Balon, 1981). In this connection, Hayes (Hayes, 1949) believes that the notion of an embryonic development stage as a certain morphological state of the embryo has no meaning at all. A different view was expressed by Vernier (Vernier, 1969) who, based on the assumption that the rate of development of the embryo may be affected not only by the temperature but also by the concentration of O_2 and the speed of the current, believes that embryonic development stages cannot be defined in terms of age or size but only on the basis of morphological and anatomical criteria.

The significance of heterochronism is certainly exaggerated (Ballard, 1973a), which is made clear by the results of experiments in which Atlantic salmon eggs were incubated at different temperatures (Gorodilov, Svimonishvili, 1979). The tendency to exaggerate it emerged in those days when developmental stages could not be distinguished with an adequate degree of accuracy. This tendency, however, still persists due mostly to the absence of diagnostic characters that would make it possible to distinguish individual stages with greater precision. In this connection, we think it necessary to explain what we understand by a stage of development.

A stage is either described as a set of morphological characters that an embryo has at a given moment, or is defined quantitatively in terms of age (in hours, days, degree days, etc.). Strictly speaking, a stage is not an interval but a moment in the process of development. Given this approach, the best way to define a stage is by specifying the time that has elapsed since the egg was fertilized. Such a definition, however, must be verified through the application of morphological criteria, because, firstly, embryos do not always

develop at the same rate and, secondly, strictly identical conditions are often very hard to recreate.

At the same time, it is difficult to view a stage defined in morphological terms as a moment of development. Even under optimum conditions, a stage would have a certain duration because morphological characters do not appear or change instantaneously. In most cases, however, diagnostic morphological characters endure for fairly indeterminate periods of time. The formation of the pectoral fins, for example, is normally distinguished as a separate stage. This is a very complex process that cannot be divided into any discrete states. It is, in other words, a continuous process, and also one whose beginning or end cannot be pinpointed with absolute certainty. For different observers, the difference in estimates of the moment of inception of the organ may amount to several days. It is, therefore, impossible to provide an accurate morphological description of any moment by using the traditional methods alone.

Hence, it is imperative for researchers to find a set of morphological characters such that would make it possible to define a stage quickly and with great accuracy. The solution of many problems in embryology depends on this. Ideally, it is desirable to reach a level of accuracy at which the period of existence of the characters identifying the stage is so short, compared to the total period of development, as to approach a moment. To achieve this, it is necessary to change from morphological criteria "of long duration" to discrete, denumerable characters and various morphological "nuances" that could serve to identify the stages. In recent years, work has been under way to find such characters for precise stage identification.

Determination of embryonic development stages during cleavage, blastulation and gastrulation. There is very little controversy as regards the early part of the cleavage period. Almost all works on embryogenesis distinguish the stages of 2, 4, 8, and sometimes 16 and 32 blastomeres. The time needed for each of these divisions accounts for only 0.3-0.4% of the length of the entire period of embryogenesis, but because these stages are so easy to distinguish, they invariably receive considerable attention.

Much more problematic is the differentiation of stages in the later part of cleavage, as well as in blastulation and gastrulation. Normally, in characterizing the stages of this period, researchers limit themselves to such vague terms as "morula", "large cell blastula", "massive yolk plug stage", etc. In view of the great interest in the early stages of development being shown by biochemists, cytologists and other specialists, the need for precise stage identification techniques is becoming increasingly urgent. Researchers involved in studies on amphibian embryos have already proposed methods for determining the number of cells in the embryo during blastulation by counting part of the surface cells on microphotographs (Signoret, Lefresne,

1971; Nakatsuji, 1974), and - during gastrulation - by measuring the width of the blastopore (Nakatsuji, 1974).

The period between fertilization and gastrulation is known in embryology as "cytotypic (cellular)", as opposed to the interval that follows, which is called "organotypic" (Ivanov, 1937). To be able to define this period in salmon embryos, we have carried out extensive cytological studies and obtained data on the rate and pattern of cell multiplication, on the parameters of the cell phases in the process of division, and on the morphology of the nuclei and cells during cleavage, blastulation and gastrulation. These data, some of which have been published (Gorodilov, Lil'p, 1978; Gorodilov, Svimonishvili, 1980, 1981), will be used to describe the stages of this period in one of our future papers.

The existing notions of the processes that take place during blastulation and gastrulation in vertebrates were formed mainly as a result of studies of the development of amphibian eggs and then used to describe the corresponding periods of development in other animals. It was assumed that these processes are similar in all animals and that they consist of a number of morphogenetic movements and interactions among the cells, which determine the overall structural configuration of the embryo. According to Ballard (Ballard, 1976, 1981), in each of the large taxonomic groups of animals (fish, amphibians, birds, etc.), blastulation and gastrulation proceed in fundamentally different ways, although they lead to the same result - the formation of the axial primordium of the embryo.

In fish, blastulation begins at the end of the 11th cleavage division with the emergence of two specialized layers of cells - the layer of surface cells (precursor of the periderm) and the periblast separating the blastoderm from the yolk (Gorodilov, Svimonishvili, 1981), and ends with the formation of the thickened margin of the blastodisc - the germ ring. Gastrulation begins with the appearance of a small thickening on the inner surface of the germ ring. According to some researchers (Pasteels, 1936), this thickening is analogous to the amphibian blastopore, through which the surface material is invaginated. Other researchers (Ballard, 1973b, c) believe that it is near this thickening that an embryonic field is formed, into which migrate cells from different parts of the blastoderm. Whichever it may be, it is along the radius of this thickening in the blastoderm that a primitive streak develops in which the axial organs are formed, while the thickening itself becomes the rear end of the developing embryo.

Simultaneously with the development of the primitive streak, the yolk is covered by the blastoderm. This process can be observed in fish embryos through the membrane of the eggs by following the movement of the germ ring, which is the front edge of the advancing blastoderm. That is why it almost invariably attracts the attention of the researchers. Observation of this process is of great practical importance since at this stage embryos are

very sensitive to external factors. It is unfortunate, however, that some researchers should try to classify the types of development of various groups of fish on the basis of the fact that their embryos reach different degrees of maturity by the time the germ ring closes (Nikiforov, 1939; Reshetnikov, 1980). In actual fact, the spreading of the blastoderm over the yolk is a secondary process which is not directly related to the development of the embryo proper: its duration depends on many factors, including the size of the yolk sac, temperature and dissolved oxygen levels. Consequently, at the time the germ ring closes, the embryos vary in maturity, which is clearly evident from the count of the pairs of somites: even in embryos from the same female the number of somites may differ by several pairs. It is obvious that the closure of the germ ring is not necessarily related in time to any particular stage of embryonic development and cannot, therefore, serve as a basis for any phylogenetic theories.

Determination of embryonic development stages during organogenesis. With the establishment of the definitive pattern of the developing embryo - the embryonic axis, a new interval, known as organogenesis, begins. This interval accounts for over 4/5 of the entire incubation period and presents particularly difficult problems as regards the selection of diagnostic characters for stage determination. Of special interest in this respect are the papers based on studies of the rainbow trout (Vernier, 1969; Ballard, 1973a). Although methodologically the studies were performed on a sufficiently high level (constant temperature during incubation; numerous illustrations in the papers), the authors' approach to distinguishing developmental stages and selecting characters for their identification after gastrulation leaves a lot to be desired. Thus, for instance, in Ballard's paper stage 18 is identified by, among other things, equality in the number of body parts attached and not attached to the yolk, stage 19 by the diameter of the pectoral fins being smaller than that of the eye cups, etc. Characters like these make it difficult to associate the stage with any particular moment.

In our studies of the incubation processes in the Atlantic salmon we set ourselves the aim of finding uniformly changing characters that could be counted or measured and then used for stage identification purposes. Two quantitative characters of this kind were discovered in the course of organogenesis: a uniform increase in the number of segments during the metamerization of the axial portion and, later, uniform growth of the embryo. Below, we are going to demonstrate how it may be possible to determine the degree of development of salmon embryos by counting their segments or measuring their length.

Determination of salmon embryo development stages in the somitogenesis period by the number of pairs of somites. In the course of our studies of salmon development we noted the rhythmicity of the

segmentation process during the metamerization of the axial portion. Several papers mention the existence of a certain periodicity in the formation of segments in various vertebrates (Price, 1934; Hamburger, Hamilton, 1951; Cooke, Zeeman, 1976), but do not report any special research into this process. We studied the rate of segmention in salmon at different constant temperatures and found that, between the time of appearance of the first pair of somites (each segment consists of a pair of somites arranged symmetrically to the right and left of the notochord) and the time of formation of the 60th-62nd pair, the segments were formed at regular, identical intervals. The formation of the last several segments proceeds at a slower rate. Altogether, 66-67 segments are formed, but later some of them apparently merge with each other, with the result that the final number of metameres in the axial portion of salmon embryos is 63-64. The total duration of the period of uniform metamerization accounts for over 1/5 of the period of embryogenesis at a constant temperature (Gorodilov, 1980). Because the process of segmentation proceeds at a uniform rate, *the count of the number of pairs of somites makes it possible to determine the stage of development and age of the embryos during the period that begins with the formation of the axial organs (before the start of the process of segmentation) and ends with the pigmentation of the eyes (62-63 pairs).*

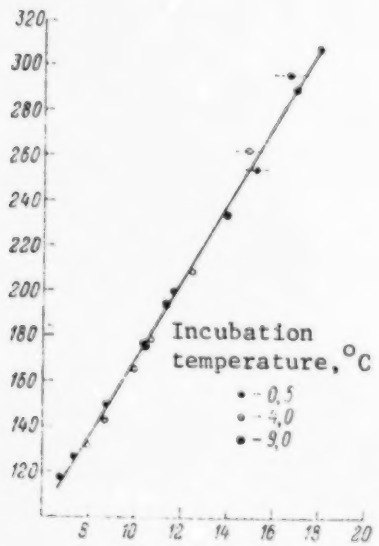
The fact that embryos are capable of producing a large number of metameres at a uniform rate is of great interest in connection with the problems of the morphogenesis of recurrent structures (Cooke, Zeeman, 1976). In practical and experimental work on embryos a recurrent interval can be used as a standard for measuring the relative length of the different embryonic stages by expressing their time span in terms of this standard.

In 1960, T.A. Detlaf and A.A. Detlaf proposed a method of measuring the duration of embryonic stages in relative units. In 1980, we proposed (Gorodilov, 1980) that a new measuring standard be used, namely the time interval during which a single pair of somites is added in the process of formation of the first 60 pairs. We designated this interval by the symbol τ_s (tau-somite). Its value can be determined by establishing the time of commencement of two stages: t_1 with the number of pairs of somites n_1, and t_2 with the number of pairs of somites n_2. Then $\tau_s = t_2 - t_1 / n_2 - n_1$, where for the salmon $n_1 \geq 1$ and $n_2 \leq 60$. The accuracy with which τ_s can be determined will grow with increase in the value of $n_2 - n_1$.

After determining the value of τ_s and taking it as a unit, we can calculate the relative length of any part of the period of embryogenesis by dividing its duration by τ_s. We were able to determine the length of certain stages in τ_s units (Gorodilov, Svimonishvili, 1979; Gorodilov, 1980) and to satisfy ourselves that it was constant at all the temperatures used in our

experiments, which shows τ_s to be perfectly adequate as a dimensionless standard.

Determination of salmon embryo development stages in the postsomitogenesis period by body length. Among the different characters that we studied during the period of development immediately following that of uniform segmentation, of particular interest from the point of view of relationship between the degree of development (age) of salmon embryos and the state of the morphological characters is the body length of the embryos. We followed all the changes that this character underwent during the period of postsomitogenesis until the hatching of the embryos. The eggs were incubated at constant temperatures of 0.5, 4.0 and 9.0°C. At each stage, we removed from 5 to 8 eggs from the incubator, opened the membranes, spread the embryos on slides and, using a magnifying glass, measured their length from the snout (at the level of the organ of smell) to the end of the tail fin. The measurements, made on graph paper, were correct to ± 0.2 mm.



Growth in length of a salmon embryo in the period of development from the time it has 60-62 pairs of somites up to the late hatching stage. X-axis: embryo body length in mm; Y-axis: age, τ_s

The results of the measurements are shown on the graph. The data obtained in the three experiments are presented here as a relationship between the growth of the embryos in length and the time of development at the corresponding temperatures. In order to present these data on a single scale, the time of development is expressed not in terms of incubation time but as an equivalent number of τ_s calculated for each temperature.

By the end of the segmentation period a salmon embryo reaches 6.5-7.0 mm in length. This length was taken as the starting point for our measurements. The data obtained in the process of subsequent development show the existence of a direct relationship between the time of incubation and the growth of the embryos: all the data fall on a straight line. This relationship was observed at all of the incubation temperatures. Since the time of incubation is expressed in τ_s, the results of the measurements made in all of the three experiments fall on a straight line.

During the observation period, from the end of somitogenesis up to the time of mass hatching, the embryos grew older by 190 τ_s. Over the same period, they grew in length from 6.7 to 18.3 mm. It is easy to see that a salmon embryo grows by 1 mm during an incubation period equivalent to the formation of approximately 17 somites.

Thus, after the end of the segmentation period and throughout the period of subsequent development up to the moment of hatching, salmon embryos grow at a uniform rate. *This makes it possible to determine the age of salmon embryos during the period between the onset of eye pigmentation and hatching by measuring the length of their bodies*.

Conclusion

The study of embryonic development is one of the most complex fields of biology. More and more researchers specializing in different areas of biology are attracted to its problems. To be able to solve them, it is necessary to have a good understanding of the principal stages of this period of ontogenesis. At present, however, the morphological and chronological sequence of events during embryonic development is still not clearly understood, which is an obstacle to more sophisticated embryo research. The Atlantic salmon is no exception: despite the long history of salmon rearing, its embryonic development has received less study than that of some other species. No chronological tables of the stages of development of the Atlantic salmon have yet been produced, although such tables are already available for many other species of fish. This paper is intended to fill this gap to a certain degree.

Most papers dealing with the problem of embryonic development stages use a purely descriptive approach: they simply report the presence of such

and such morphological characters. The methodological level of these papers is pretty low. We are not aware, for example, of any studies in which the development of salmon embryos was investigated at constant temperatures. Analytical methods are almost never used. The choice of characters is often arbitrary. The characters in most cases have no discrete states and no clearly defined time limits. All this constitutes a great limitation: embryonic development being an exceedingly dynamic process, the establishment of the relationship between the characters and the different developmental stages is of great importance to successful research.

A constant environment makes it possible to follow the progress of embryonic development by measuring the time of incubation of the eggs. But, as we said before, even in this case the division into stages must be verified on the basis of morphological characters. The latter are the most reliable criteria for stage identification. It is believed that changes in the environment may bring about changes in the sequence in which morphological characters normally develop (Hayes et al., 1953; Meshkov, Lebedeva, 1977 ; Balon, 1981). In our studies of the process of incubation of salmon eggs under different ambient conditions we never came across a single instance of heterochronism of morphological characters. Changes were observed in the time of emergence of only those characters that develop as a result of physiological reactions: the formation of bile in the intestines, integument pigmentation, etc. But structural morphological characters conform to a very strict "schedule" and no changes ever take place in the sequence in which they appear. The mistaken belief that heterochronism is a common phenomenon has arisen as a result of the use of characters with ill-defined time limits.

The task of embryologists is to determine reliable morphological indices that could be used for sufficiently accurate stage identification. For this, they must find index characters that exist for a very short time: the magnitude of error in identifying a stage is directely correlated with the "life span" of its morphological index characters*.

Over a short period of time salmon embryos make the transition from single-celled to almost fully developed organisms. Obviously, the principles of stage determination must differ depending on the period of development the embryos are undergoing at the time the study is being made. If it is conducted during the cytotypic period (Ivanov, 1937), it must apparently take into account such cytological characters as the numer of cells, their differentiation indices and the morphology of the cell structures. Naturally,

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* The generally accepted notion of the duration of a stage as the time between the fertilization of the egg and the emergence of the index character of this stage must not be confused with the life span of the character itself, the inclusion of which in the duration of the stage is a mistake in the definition.

use must also be made of characters related to the outward shape of the embryo during blastulation and gastrulation.

After the formation of the embryonic axis at the very end of the gastrulation period, the development of salmon embryos can be monitored by counting the number of pairs of somites (from 1 to 60-62), because they are formed at a uniform rate. It is obvious that during this period up to 60 discrete states (stages) can be distinguished on the basis of morphological criteria, which is very important because the process of somitogenesis is accompanied by the formation of almost all of the principal organs and functional systems of the organism. Thanks to the uniform rate of the process of segmentation (somitogenesis), the number of segments can serve as a convenient chronological index for determining the age of the embryos (Gorodilov, 1980).

After the process of segmentation is over and up to the moment of hatching, the age of the embryos can be determined on the basis of their length, because under constant conditions growth by one unit of length takes the same amount of time. Until more reliable morphological characters are found for this period of development, there is every reason to make use of the body length index for determining the age of the embryo. This index was used for the same purpose in studies performed by other researchers (Knight, 1963; Vernier, 1969), including studies of salmon (Yandovskaya et al., 1979), but the relationship between time and embryo growth was never made the subject of any special investigation.

Based on what has been said above, the entire process of embryogenesis in the salmon can (somewhat arbitrarily) be divided into five periods, which differ in the choice of criteria for stage identification.

1. Cleavage. Criteria for stage identification: the number of blastomeres, cytological data.

2. Blastulation. Criteria for stage identification: the shape of the blastodisc, cytological data.

3. Gastrulation. Criteria for stage identification: the shape and structure of the embryonic field (but not the spread of the blastoderm over the yolk).

4. Somitogenesis. Criteria for stage identification: the number of pairs of somites.

5. Uniform linear growth of the embryo.

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